Three new genera of misophrioid copepods from the near-bottom plankton community in the North Atlantic Ocean

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Introduction

Only three species of the copepod order Misophrioida have been described, *Misophria pallida* Boeck 1864, *Benthomisophria palliata* Sars 1909 and *B. cornuta* Hulsemann & Grice 1964. Despite the small number of species the misophrioids have attracted interest because of the combination of characters that they exhibit, drawn from both the gymnoplean and podoplean lineages within the Copepoda. Attention has recently been drawn to the unique characters that misophrioids display; the possession of a carapace-like posterior extension of the cephalosome, the lack of a nauplius eye in a free living copepod, the distensibility of the gut and the retention of the antennary glands as the functional excretory organs of the adult (Boxshall, 1982). These characters, together with the abbreviated lecithotrophic nauplius phase of the life cycle, can be interpreted collectively as evidence of a bathypelagic origin of the Misophrioida. This interpretation is supported by the discovery of several new misophrioid taxa from the deep North Atlantic Ocean, which was reported at the First International Conference on Copepoda held at Amsterdam in August 1981 (Boxshall, in press).

A total of 37 misophrioids was taken in a single haul fished near the bottom in 3000 m of water to the south west of the Azores. Fourteen of these were *B. cornuta,* 8 were *B. palliata* and 15 represented previously undescribed taxa. Three new genera and species are here described on the basis of 13 of these specimens, the remaining 2 specimens being too badly damaged for description. The new genera are of great phylogenetic significance as they exhibit some very plesiomorphic characters which provide fresh insights on the nature of the appendages of the common ancestor of the Copepoda as a whole. The new records of *B. cornuta* and *B. palliata* further extend their known geographical ranges.

Family **MISOPHRIIDAE**

Genus ***ARCHIMISOPHRIA*** nov.

DIAGNOSIS. As for type species.

TYPE SPECIES. *Archimisophria discoveryi* gen. et sp. nov.

Archimisophria discoveryi gen. et sp. nov.

Adult female (Fig. 1A) body length 1·1 to 1·4 mm. Prosome large, apparently 4-segmented but with first free thoracic somite entirely concealed beneath a carapace-like extension from the posterior margin of the maxilliped-bearing somite. Nauplius eye absent. Prominent anteriorly-directed rostrum visible from dorsal aspect, not fused to labrum (Fig. 1B). Cone organs not observed but large mass of glandular tissue present on sides of cephalosome beneath usual location of cone organs. Urosome 6-segmented (Fig. 1C). Surface

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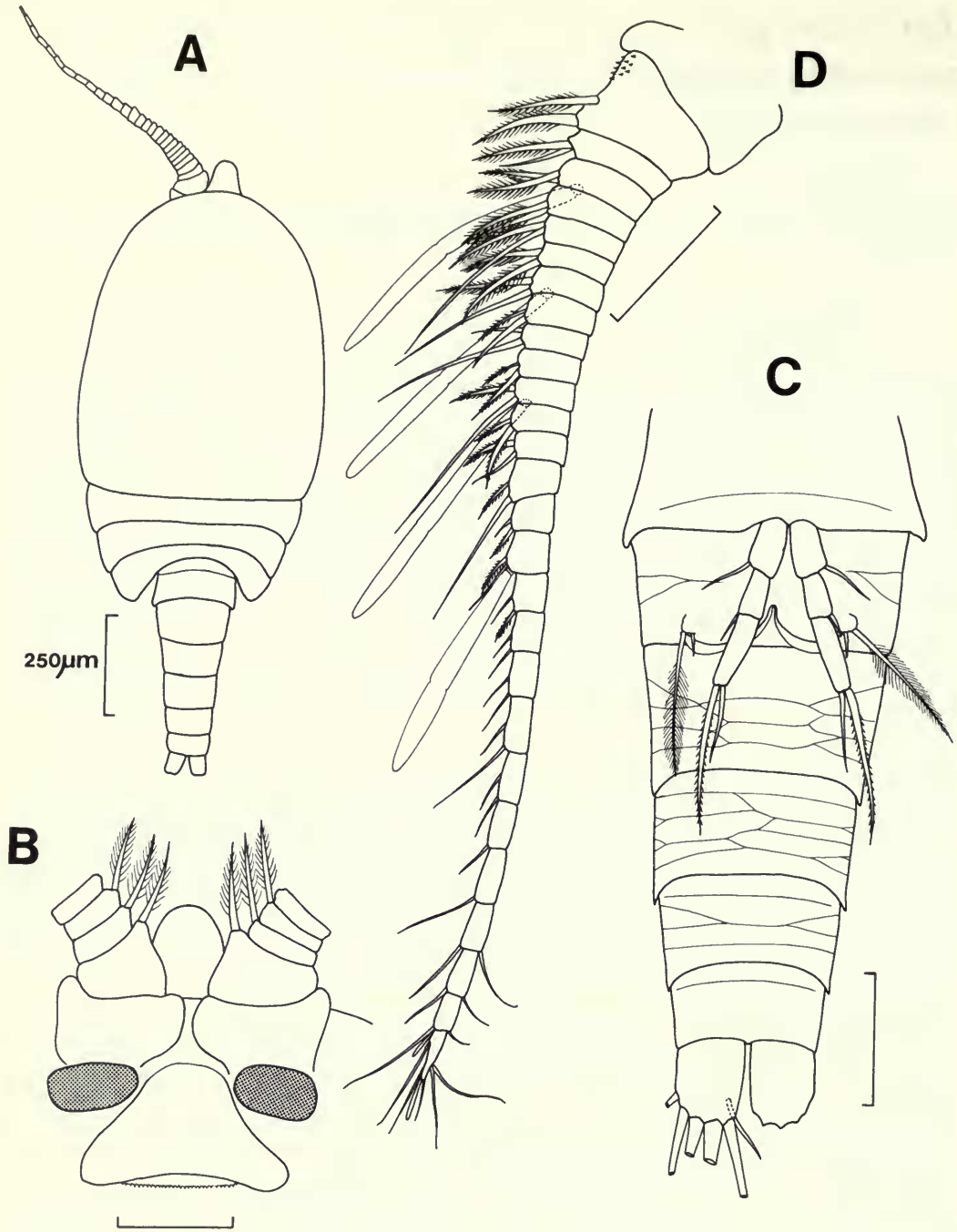

Fig. 1 *Archimisophria discoveryi* gen. et sp. nov. Holotype ♀. A, dorsal view; B, rostrum and labrum, ventral; C, urosome, ventral; D, antennule, dorsal. Scales 100 µm unless otherwise stated.

of prosome and urosome somites 1 to 5 ornamented with a reticulum of epicuticular lamellae. Urosome somite 6 without reticulate markings. Caudal rami longer than wide; armed with 2 long distal margin setae, 2 medium-length distal angle setae, a dorsal seta near the inner margin and a distally located lateral seta.

Antennule (Fig. 1D) 27-segmented, articulating proximally with an expanded area of ventral cephalic surface (Fig. 1B). Armature elements as follows: I–2, II–2, III–2+1 aesthetasc, IV–2, V–2, VI–2, VII–2+1 aesthetasc, VIII–2, IX–2, X–2, XI–2+1 aesthetasc, XII–2, XIII–2, XIV–2, XV–2, XVI–2+1 aesthetasc, XVII–2, XVIII–2, XIX–2, XX–2, XXI–2, XXII–1, XXIII–1, XXIV–2, XXV–2, XXVI–2+1 aesthetasc, XXVII–5+1 aesthetasc. First segment also with patch of minute spinules.

Labrum (Fig. 1B) small, posteriorly directed, not fused with rostrum, with a posterior row of marginal denticles.

Antenna (Fig. 2A), basis lacking inner distal seta; endopod 3-segmented, exopod 8-segmented. Endopod segment 1 apparently unarmed; segment 2 with 4 unequal unilaterally plumose setae at inner distal angle; segment 3 with 6 long subequal unilaterally plumose setae along distal margin and with several transverse rows of spinules. Exopod segment 1 with a short naked seta at inner distal angle; segments 2 and 3 unarmed; segment 4 with a long plumose seta at inner distal angle; segment 5 with 2 long plumose setae on inner margin; segments 6 and 7 small, unarmed; segment 8 with 3 long unilaterally plumose setae on distal margin and areas of spinules subapically.

Mandible (Fig. 2B) with well developed gnathobase bearing distally 2 multicusped blades, 5 strong spines and an extensive fringe of pinnules. Mandibular palp comprising basis, 2-segmented endopod and 4-segmented exopod. Basis armed with a naked seta at inner distal angle. Endopod segment 1 with a short unilaterally plumose seta at inner distal angle; segment 2 with 8 unequal plumose setae along distal margin. Exopod segment 1 unarmed; segments 2 and 3 each with 1 long seta at inner distal angle; segment 4 with 3 similar unilaterally plumose setae and a short naked seta.

Maxillule (Fig. 2C), gnathobase with 14 distal elements; endite 1 with 1 spiniform and 3 setiform armature elements, endite 2 with 3 spiniform elements. Outer lobe rudimentary, represented by 6 plumose setae on outer surface of segment. Maxillulary palp biramous with 2-segmented endopod and 1-segmented exopod. Endopod segment 1 with 3 unequal armature elements at inner distal angle; segment 2 with a long and a short seta proximally on inner surface and an apical armature of 3 long unilaterally plumose setae, 1 long and 2 short naked setae. Exopod with a proximal fringe of pinnules and 6 plumose setae on inner margin and with 3 long unilaterally plumose setae and a naked seta on distal margin.

Maxilla (Fig. 3A) 6-segmented; segment 1 with 6 plumose setae on proximal endite and 3 on distal endite; segment 2 with 3 similar setae on both proximal and distal endites; segment 3 produced medially into a curved claw armed with 3 naked setae near its base; segments 4 to 6 with a total of 10 setae.

Maxilliped (Fig. 2D) 8-segmented, with a 3-segmented, robust proximal portion and a slender 5-segmented distal portion. Segment 1 with 1 seta on inner surface; segment 2 with 2 medial setae and a row of pinnules along the outer margin; segment 3 with proximal endite bearing 1 strong spine and 3 setae, distal endite with 1 naked seta and a long plumose seta, 2 other setae on inner margin, a plumose seta at inner distal angle and a long row of pinnules along outer margin; segments 4 to 6 with 1, 2 and 1 medial setae respectively, each armed with short spinules; segment 7 with an inner margin spinulate seta and an outer plumose seta on which the pinnules decrease markedly in length towards the apex; segment 8 with 3 similar plumose setae and a naked seta.

Legs 1 to 4 incomplete in holotype ♀ and paratype ♀, assumed to be similar to those described below for a paratype ♂.

Leg 5 (Fig. 1C) uniramous, 3-segmented and positioned midventrally with inner margins almost touching at base. Segment 1 with 1 naked seta at outer distal angle; segment 2 with a short naked seta in same position; segment 3 elongate with 2 unequal distal margin setae, the longer armed with spinules bilaterally.

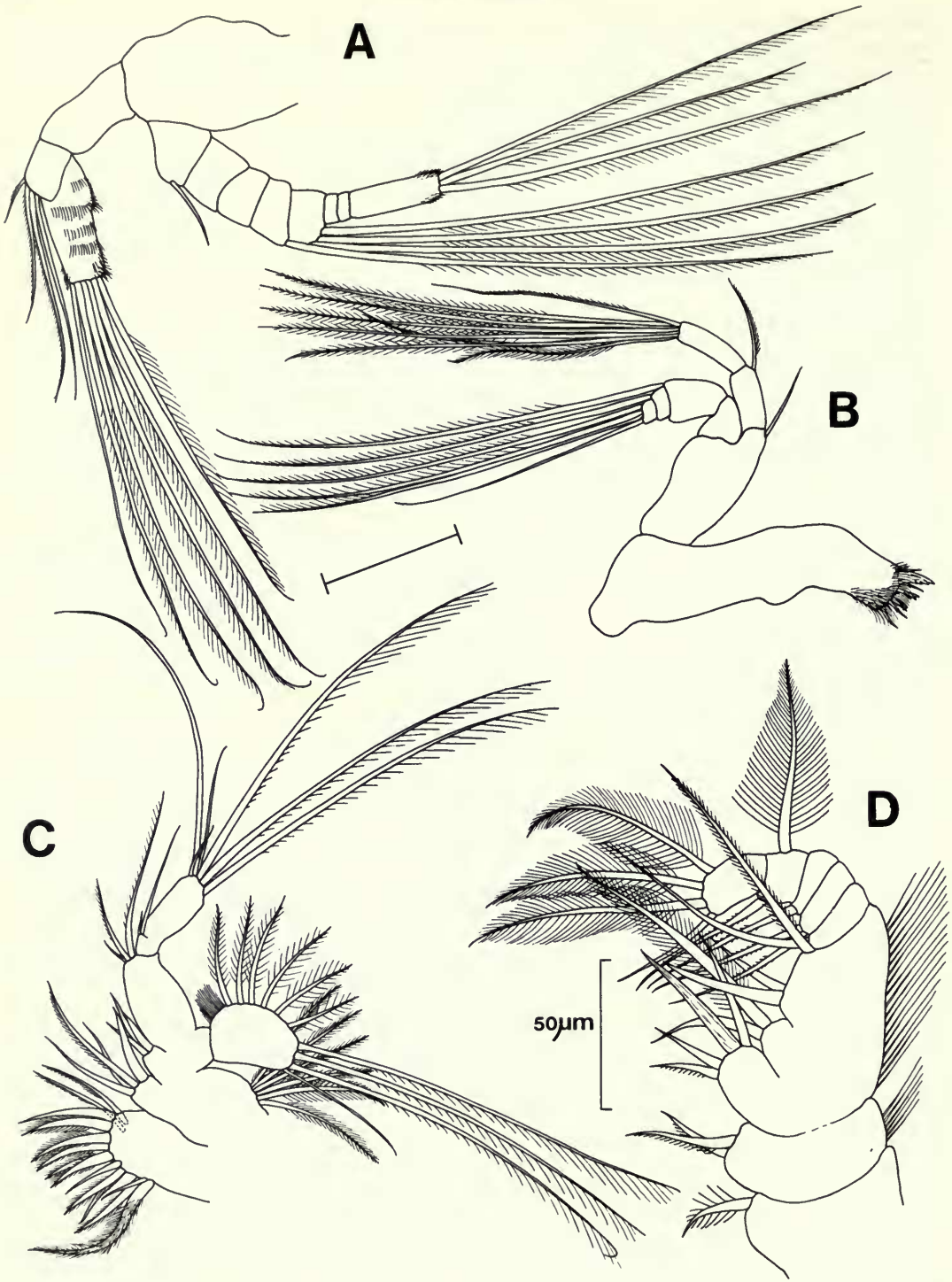

Fig. 2 *A. discoveryi.* A, antenna, anterior; B, mandible, anterior; C, maxillule, posterior; D, maxilliped, posterior. Scales 100 µm unless otherwise stated.

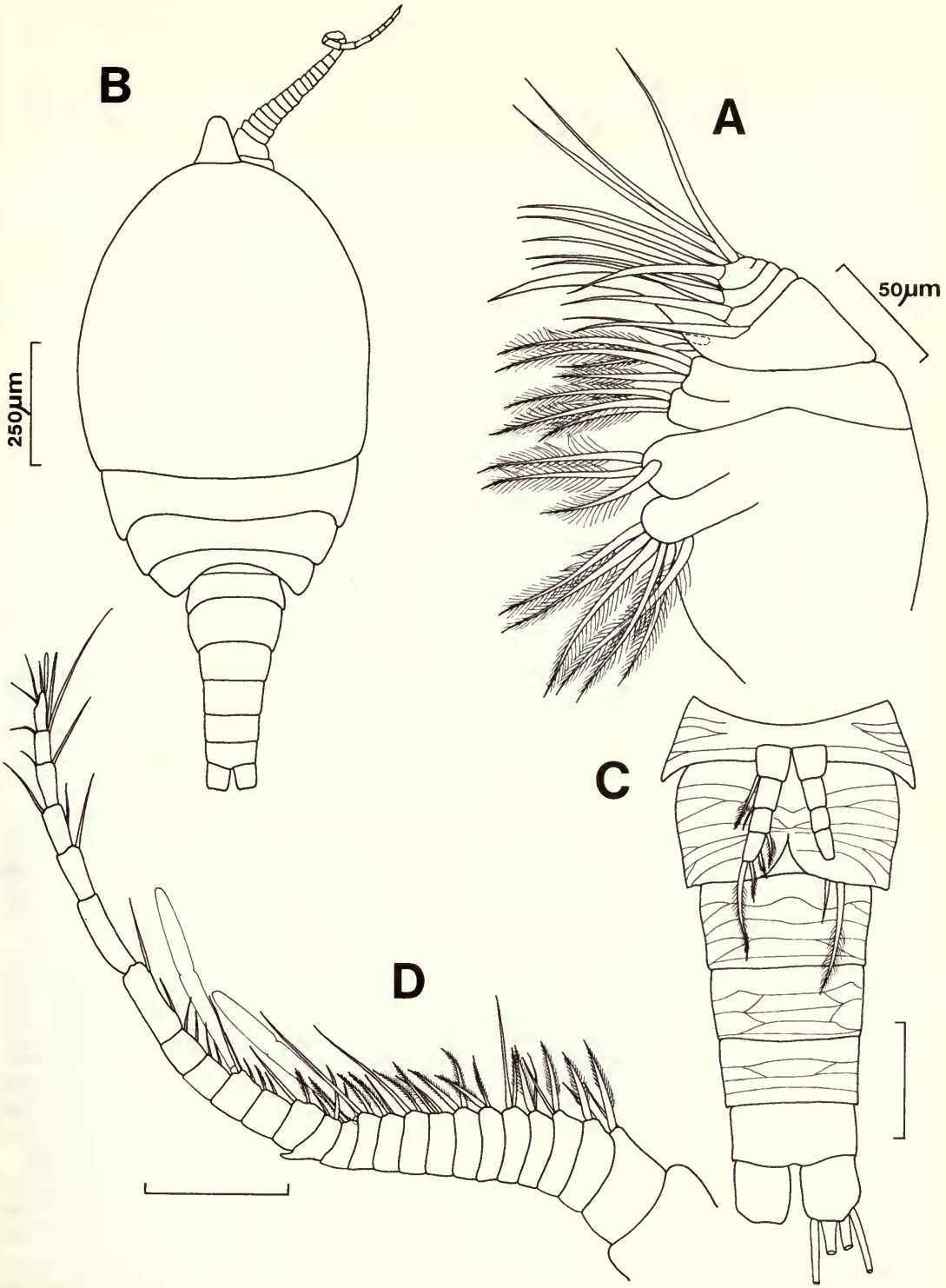

Fig. 3 *A. discoveryi.* A, maxilla, anterior; B, Paratype ♂, dorsal view; C, urosome, ventral; D, antennule, dorsal. Scales 100 μm unless otherwise stated.

Leg 6 (Fig. 1C) reduced to a semicircular flap closing off the opening of the genital antrum; bearing an outer plumose seta and a short inner spine.

Adult male (Fig. 3B) body length 1·1 to 1·3 mm (based on 3 specimens). Prosome and urosome (Fig. 3C) as in adult female. Appendages as in female except for antennules and legs 5 and 6.

Antennules (Fig. 3D) 25-segmented, unigeniculate with the articulation between segments XIX and XX. Armature elements as follows: I–2, II–2, III–2, IV–2, V–2, VI–2, VII–2, VIII–2, IX–2, X–2, XI–2+1 aesthetasc, XII–2, XIII–2, XIV–2, XV–4, XVI–2+1 aesthetasc, XVII–2, XVIII–2, XIX–2, XX–0(?), XXI–1, XXII–2, XXIII–2, XXIV–2+1 aesthetasc, XXV–3+1 aesthetasc. Segment XIII with a spinous process at posterolateral angle.

Legs 1–4 (Figs 4A-D) biramous with 3-segmented rami; armature formula as follows:

	coxa	basis	endopod	exopod
leg 1	0–1	I–1	0–1;0–1;1,2,3,	I–1;I–1;III,I,3
leg 2	0–1	I–0	0–1;0–2;1,2,3	I–1;I–1;III,I,4
leg 3	0–1	1–0	0–1;0–2;1,2,3	I–1;I–1;III,I,4
leg 4	0–1	1–0	0–1;0–2;missing	I–1;I–1;III,I,4

Pinnule rows present on inner and outer margins of endopod segments and inner margins of exopod segments; spinules present along margins of exopod segments. All outer margin exopodal spines armed with bilateral strips of fine membrane, apical spine with membrane externally and pinnules internally. All setae plumose except for distalmost 2 inner margin setae on exopod of leg 4. These setae with blunt tips and rows of short stout pinnules, possibly representing a male dimorphic character.

Leg 5 (Fig. 4E) uniramous, 4-segmented and with bases of legs almost touching at ventral midline as in ♀. Segment 1 bearing 1 plumose seta at outer distal angle; segment 2 with naked seta in same position; segment 3 with plumose seta at inner distal angle; segment 4 with short inner margin plumose seta and 2 unequal plumose setae on distal margin.

Leg 6 (Fig. 3C) represented by a flattened plate bearing a long outer plumose seta and a short inner spine.

MATERIAL EXAMINED. Holotype ♀, 3 paratype ♂♂, 1 ♀, 2 Copepodid IV and 3 Copepodid III stages all from *Discovery* Stn 10379#37 (34°57′ N 32°55′ W) in the North Atlantic to the southwest of the Azores. Collected in RMT1+8M net system fished 23 to 56 m off the bottom in a water depth of about 3000 m. BM(NH) Registration Nos Holotype ♀ 1982.128, paratype ♀ 1982.129, ♂♂ 1982.130–132, Co. IV 1982.133–134 and Co. III 1982. 135–137.

REMARKS. The new genus differs from all known misophrioids, including those described herein, in the possession of an anteriorly directed rostrum. In other genera the rostrum is either ventrally directed (*Misophria* and *Misophriopsis* gen. nov.) or posteroventrally directed and fused to the labrum *(Benthomisophria* and *Misophriella* gen. nov.). Another remarkable feature of this genus is the large number of segments in the antennules of both sexes. The twenty-seven segments found in the female is the largest number recorded for any copepod, including the calanoids in which 25 is the largest number known. The phylogenetic significance of the multi-segmented antennules is discussed below.

The developmental stages of *A. discoveryi* will not be described as only the third (Co. III) and fourth (Co. IV) copepodid stages have been found. As in other misophrioids (Boxshall & Roe, 1980) the copepodid stages can be determined by the number of urosome somites, the Co. III having 3 and the Co. IV having 4. It is interesting to note that the segmentation of the antennule is complete (27 segments) at the Co. IV stage whereas in *Benthomisophria palliata* the complete complement of 18 segments is not achieved until the last moult into the adult. The third copepodid of *A. discoveryi* has a 24-segmented antennule.

The presence of a 3-segmented leg 5 in female and 4-segmented leg 5 in male *A. discoveryi*

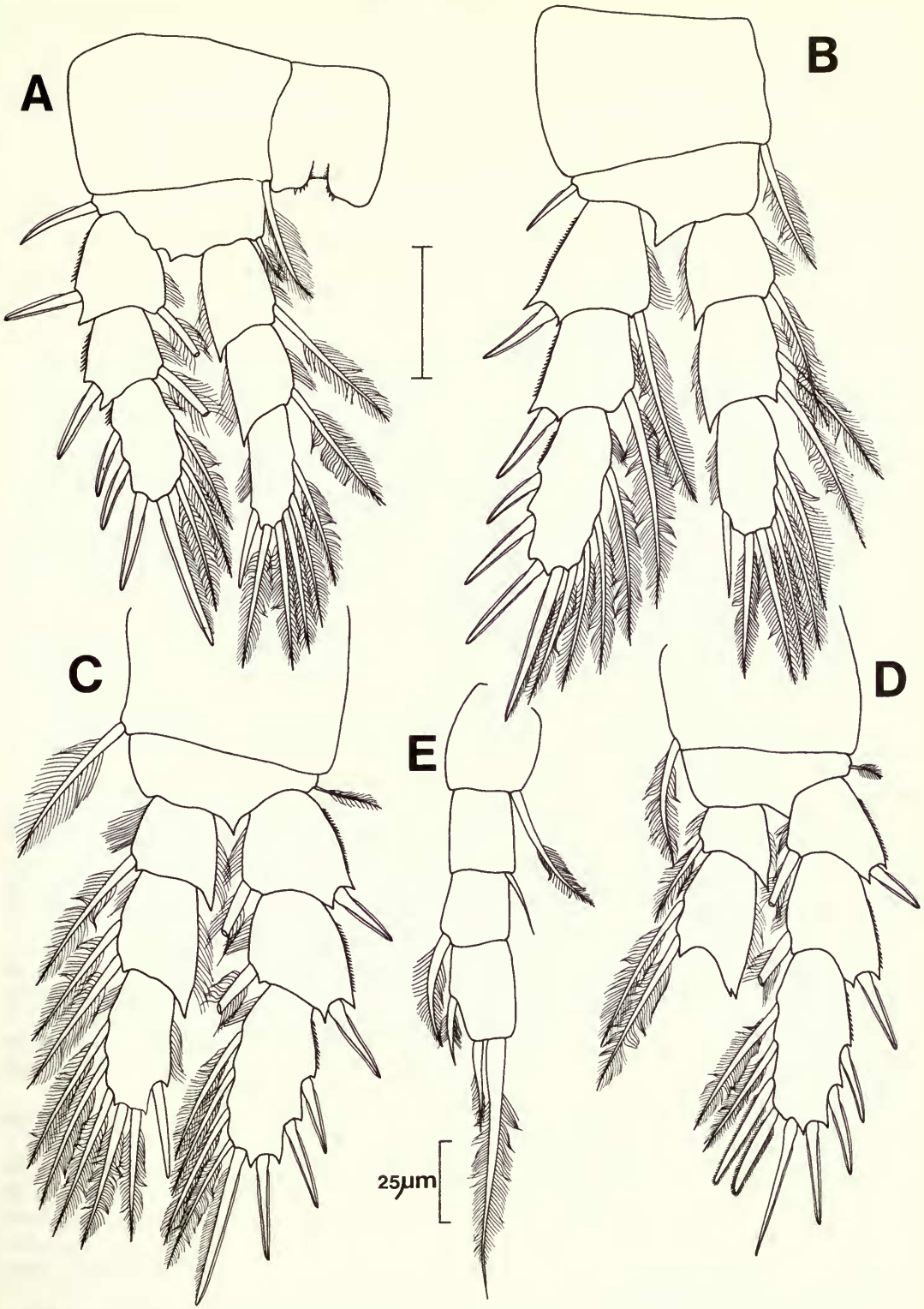

Fig. 4 *A. discoveryi.* A, leg 1, anterior; B, leg 2, anterior; C, leg 3, anterior; D, leg 4, anterior; E, leg 5, anteroventral. Scales 100 µm unless otherwise stated.

is the first documented example of sexual dimorphism in the fifth leg in misophrioids. In *Misophria* and *Benthomisophria* sexual dimorphism is restricted to the antennules and sixth legs. The presence of modified setae on the inner margin of the third exopod segment of leg 4 in male *A. discoveryi* may also represent sexual dimorphism but this cannot be confirmed until more material is obtained, as the only 2 females in the present material had incomplete fourth legs.

Genus *MISOPHRIELLA* nov.

DIAGNOSIS. As for type species.

TYPE SPECIES. *Misophriella tetraspina* gen. et sp. nov.

Misophriella tetraspina gen. et sp. nov.

Adult female (Fig. 5A) body length 0·87 mm (Holotype ♀). Prosome apparently 4-segmented but, as in all misophrioids, with the first free thoracic somite entirely concealed beneath a carapace-like extension of the posterior margin of the maxilliped-bearing somite. Nauplius eye absent. Rostrum posteroventrally directed and fused to anterior surface of labrum, not visible from dorsal aspect. Cone organs present in lateral areas on cephalosome. Urosome 6-segmented (Figs 6A-B), somites 2 to 5 each with a hyaline frill around posterior border. Anal somite with paired lobes dorsally, either side of anus and row of minute spinules around posterior margin. Pairs of pores present on both dorsal and ventral surfaces of anal somite. Caudal rami about as long as wide, armed with 2 long distal margin setae, 2 medium length distal angle setae, a dorsal seta near the distal margin, a seta near the middle of the lateral margin and a proximal setule on this margin.

Antennule (Fig. 5B) 19-segmented, articulating basally with a raised area of ventral cephalic surface. Armature elements as follows: I–1, II–9, III–2, IV–2, V–6, VI–2, VII–2, VIII–2, IX–2 + 1 aesthetasc, X–2, XI–2 + 1 aesthetasc, XII–2, XIII–2, XIV–2 + 1 aesthetasc, XV–1, XVI–1, XVII–2, XVIII–2 + 1 aesthetasc, XIX–6 + 1 aesthetasc. Segment I with 1 and segment II with 3 strong curved setae, each strongly sclerotized with an expanded base and a row of spinules along its convex margin.

Labrum large, posteriorly directed and fused with rostrum.

Antenna (Fig. 5C); basis with inner distal seta; 3-segmented endopod and 6-segmented exopod. Endopod segment 1 with a short plumose seta at inner distal angle; segment 2 with 2 short naked setae near middle of inner margin and a long and a short seta at inner distal angle; segment 3 with 6 long unilaterally plumose setae along its distal margin. Exopod segment 1 unarmed; segments 2 to 5 each with a single long, unilaterally plumose seta on its inner margin; segment 6 with 2 similar setae and a short plumose seta on its distal margin.

Mandible (Fig. 7A) with well developed gnathobase bearing 4 multicusped blades and some pinnules distally. Mandibular palp comprising basis, 2-segmented endopod and 4-segmented exopod. Basis apparently lacking inner distal angle seta. Endopod segment 1 with 1 naked seta at inner distal angle; segment 2 with 1 short naked seta and 4 long plumose setae apically. Exopod segment 1 unarmed; segments 2, 3 and 4 with 1, 2 and 3 long plumose setae respectively.

Maxillule (Fig. 7B) with armature of gnathobase reduced, comprising only 7 curved spinous elements, 1 hirsute seta and 2 slender naked setae. Endites 1 and 2 with 5 and 4 slender setae respectively; all setae sparsely armed with short spinules bilaterally. Outer lobe apparently absent. Maxillulary palp biramous with 1-segmented exopod and 3-segmented endopod. Endopod segment 1 fused to basis, with 3 unequal plumose setae at inner distal angle; segment 2 with 2 inner margin plumose setae; segment 3 small, bearing 4 unequal setae apically. Exopod with 3 long plumose setae distally and a short plumose seta and a row of pinnules along inner margin.

Maxilla (Fig. 7C) 6-segmented; segment 1 with 2 hemispherical endites, proximal endite with 1 naked and 4 plumose setae, distal endite with 2 spinulate setae; segment 2 with a

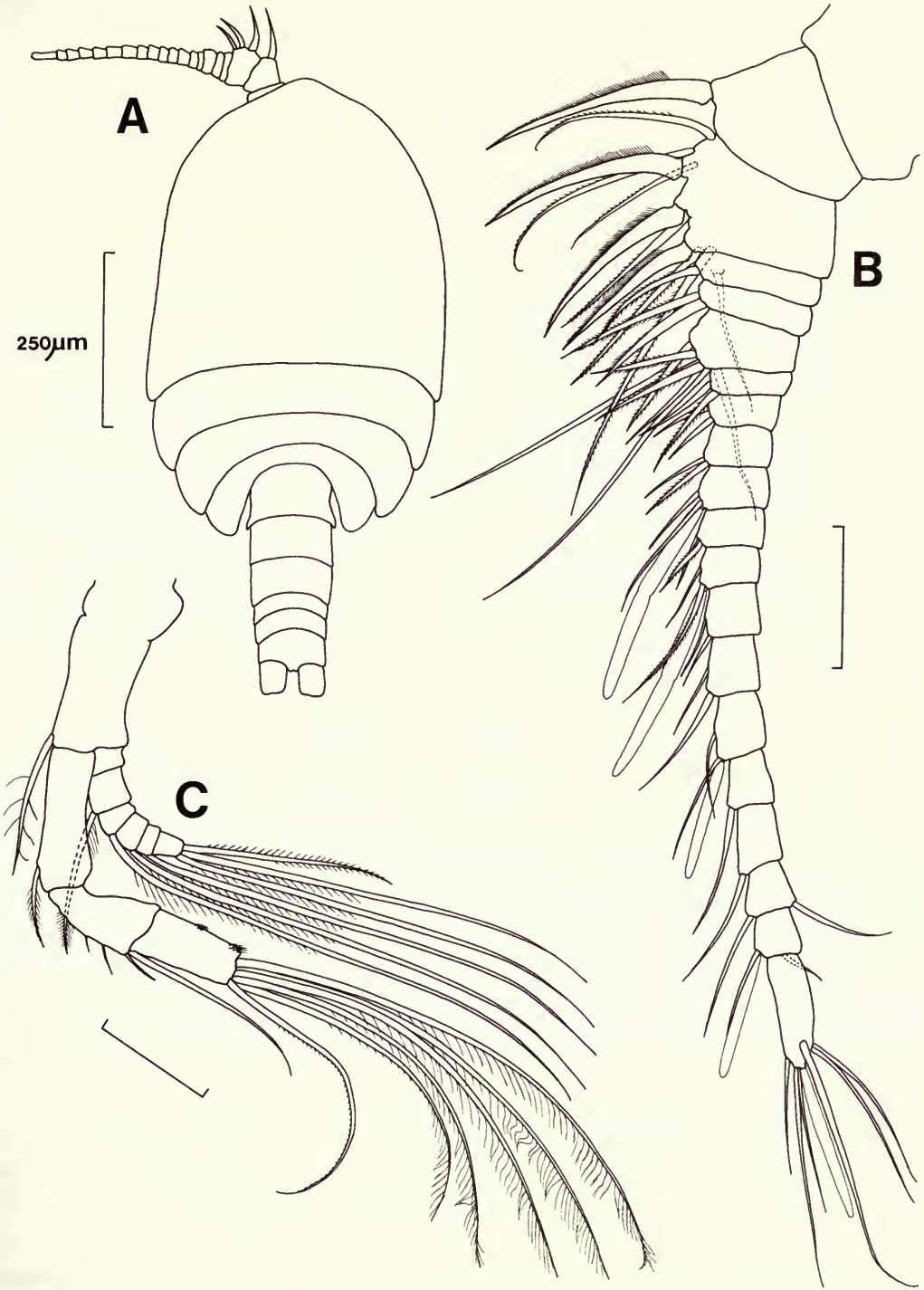

Fig. 5 *Misophriella tetraspina* gen. et sp. nov. Holotype ♀. A, dorsal view; B, antennule, dorsal; C, antenna, anterior. Scales 50 µm unless otherwise stated.

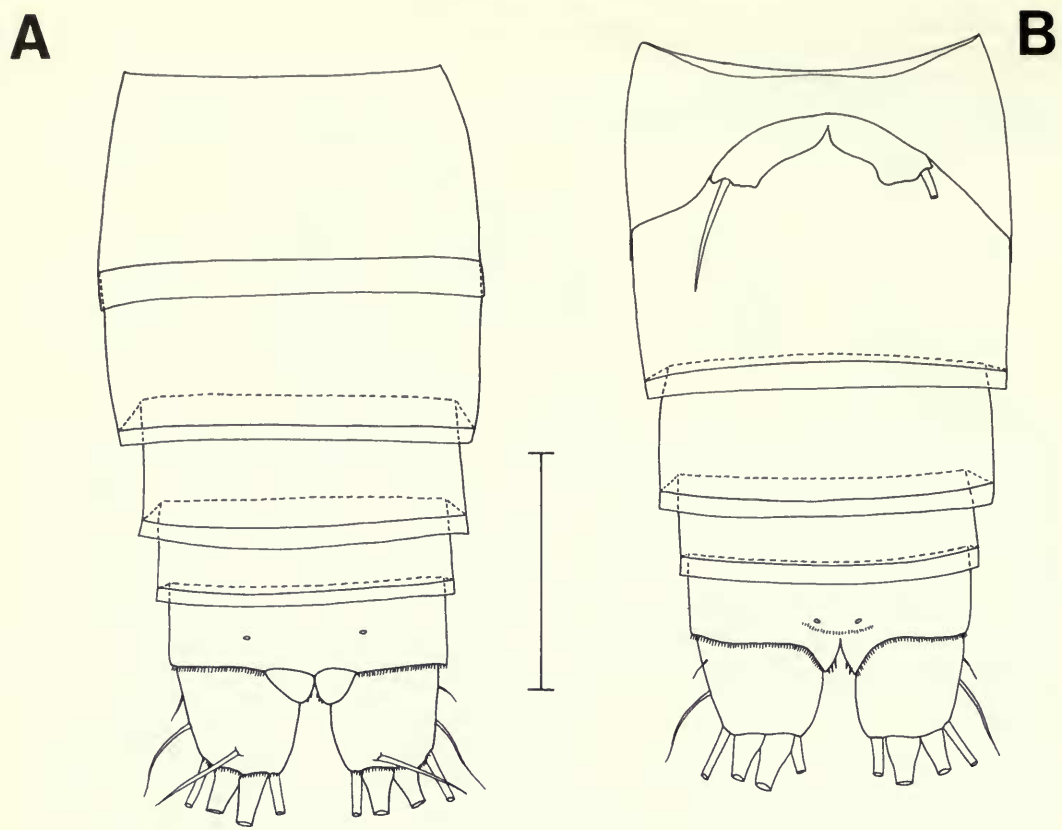

Fig. 6 *M. tetraspina.* A, urosome, dorsal; B, urosome, ventral. Scale 100 μm.

single elongate endite bearing 3 unequal naked setae at its apex; segment 3 produced into a long medial claw with a fringe of minute pinnules along its concave margin and 3 setae near its base; segments 4 to 6 each with 1 long, robust claw-like seta armed with a fringe of pinnules, segment 6 also bearing 2 slender apical setae.

Maxilliped (Fig. 7D) 7-segmented; segments 1 and 2 long and robust. Segment 1 armed with 1 proximal seta, 3 midmargin setae and 2 distal setae all on inner margin; segment 2 with 3 slender setae at middle of inner margin; segments 3 to 5 with 1, 2 and 1 slender inner margin setae respectively; segment 6 with an articulated seta distally and segment 7 with 2 similar articulated setae, plus 2 short naked setae.

Legs 1–4 (Figs 8 A-D) biramous, presumably with 3-segmented rami; armature formula as follows:

	coxa	basis	endopod	exopod
leg 1	0–1	1–1	0–1;0–2;1,2,3	I–1;I–1;III,I,4
leg 2	0–1	1–0	0–1;missing	I–1;I–1;missing
leg 3	0–1	1–0	0–1;0–2;missing	I–1;missing
leg 4	0–1	1–0	0–1;0–2;missing	I–1;missing

Pinnule rows present on inner and outer margins of endopod segments and on inner margins of exopod segments. Leg 1 with accessory digitiform processes on outer margin of exopod segments 2 and 3 between bases of spines. Exopod spines armed with bilateral strips of serrate membrane.

Leg 5 (Fig. 8E) uniramous, 4-segmented. Segment 1 broader than long, unarmed; segment

2 broader than both segments 1 and 3, armed with a naked seta on outer margin; segment 3 with spinous process at outer distal angle; segment 4 with 1 plumose seta either side of central spine in distal margin, also with an inner margin plumose seta on left leg but not on right.

Leg 6 (Fig. 6B) forming a curved plate on ventral surface of genital somite; armature incomplete.

MATERIAL EXAMINED. Holotype ♀ collected at *Discovery* Stn 10379#37 (34°57′ N 32°55′W) in the North Atlantic southwest of the Azores. Caught in RMT1+8M net system fished 23 to 56 m off the bottom in a water depth of about 3000 m. BM(NH) Registration No. 1982·138.

REMARKS. The new genus differs from all known misophrioids, including those described herein, in the form of the maxillule (which has a 3-segmented endopod, no outer lobe and an elongate exopod bearing only 4 setae), in the presence of only a single endite on the second segment of the maxilla and in the number of segments in the antennule. This genus exhibits a general reduction in the numbers of armature elements on most of the mouthparts, particularly on the maxillulary palp and the maxilla. In addition to these quantitative differences there are also qualitative differences, such as the spiniform nature of 4 setae on the proximal segments of the antennule and the presence of articulated setae on the maxilliped.

The armature elements of the fifth legs provide some indication of the homology of the segments. The second segment carries an outer seta at its distal angle and it is also much wider than the other segments. It probably represents the basis. Segment 1 therefore represents the coxa, and segments 3 and 4 the 2-segmented exopod. The holotype exhibits bilateral asymmetry in the armature of leg 5 but it is assumed that this is an aberrant condition and is not indicative of a true asymmetry as displayed by the fifth legs of many calanoids.

Genus ***MISOPHRIOPSIS*** nov.

DIAGNOSIS. As for type species.

TYPE SPECIES. *Misophriopsis dichotoma* gen. et sp. nov.

Misophriopsis dichotoma gen. et. sp. nov.

Adult female (Fig. 9A) body length 0·9 mm (Holotype ♀). Prosome apparently 4-segmented but with first free thoracic somite entirely concealed beneath a carapace-like extension from the posterior margin of the maxilliped-bearing somite. Nauplius eye absent. Rostrum small, ventrally directed with its apex adjacent to, but not fused to, the labrum (Fig. 12). Cone organs present in lateral areas on either side of cephalosome. Urosome (Fig. 9B) 6-segmented. Caudal rami wider than long, armed with 2 long distal margin setae, a medium length seta at both inner and outer distal angles, another on the dorsal surface near bases of distal setae, and a short lateral seta.

Antennule (Fig. 9C) 18-segmented. Armature elements as follows: I–1, II–11, III–2, IV–6, V–2, VI–2, VII–2, VIII–2+1 aesthetasc, IX–2, X–2+1 aesthetasc, XI–2, XII–2, XIII–2+1 aesthetasc, XIV–1, XV–1, XVI–2, XVII–2+1 aesthetasc, XVIII–6+1 aesthetasc. Spinules present on posterior surface of segment II.

Labrum (Fig. 12) large, posteriorly directed but not fused with rostrum; armed with 2 large medially directed spinous processes on its posterior margin.

Antenna (Fig. 9D) basis lacking inner distal seta; endopod 3-segmented, exopod 6-segmented. Endopod segment 1 with 2 inner distal setae; segment 2 with 3 setae spaced along inner margin; segment 3 with 5 long distal margin setae. Exopod segment 1 unarmed; segment 2 with 2 inner margin setae; segments 3 to 5 each with a single seta at inner distal angle; segment 6 with 3 plumose setae.

Mandible (Fig. 9E) with well developed gnathobase bearing distally 4 multicusped blades,

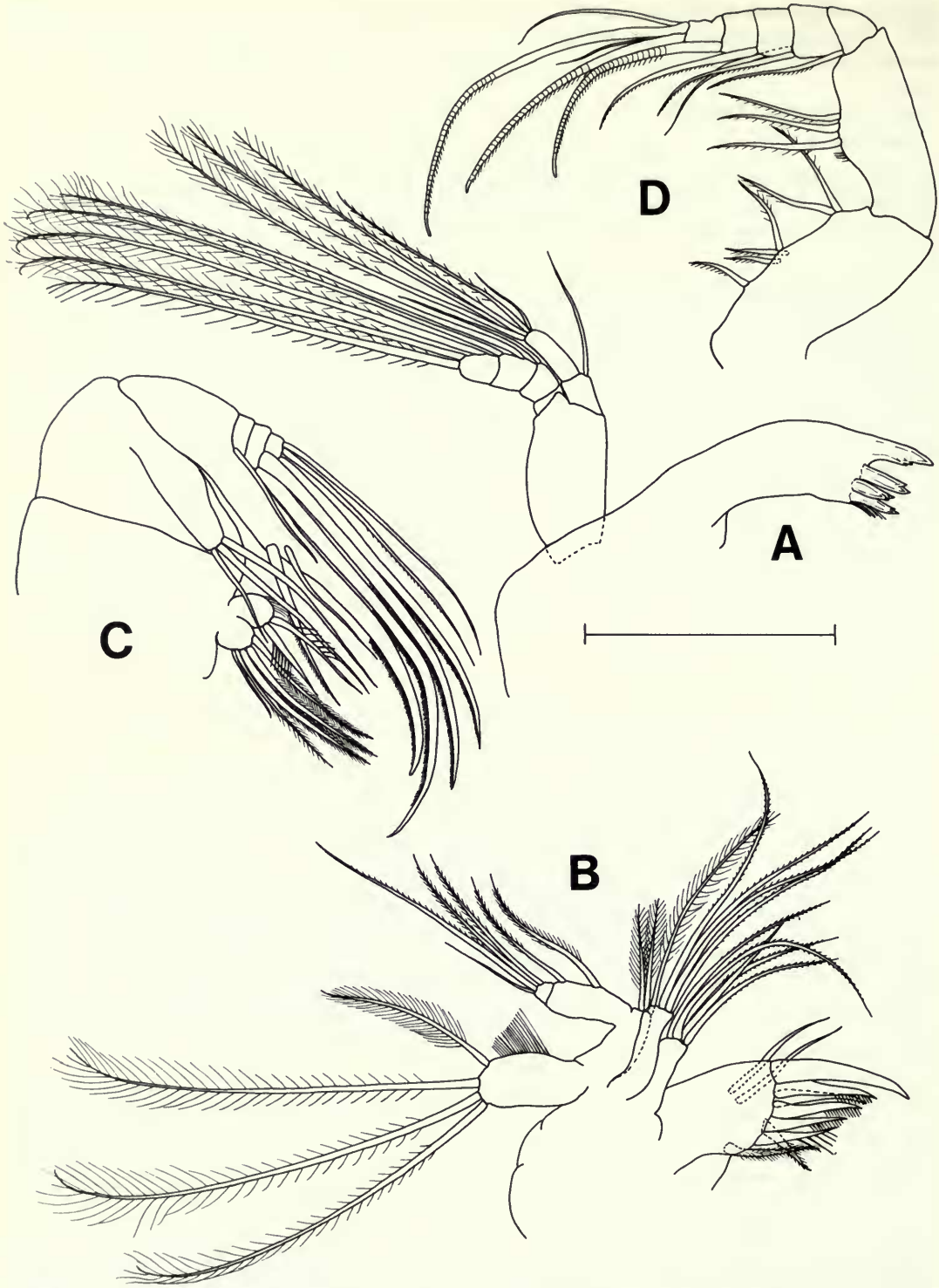

Fig. 7 *M. tetraspina.* A, mandible, anterior; B, maxillule posterior; C, maxilla, anterior; D, maxilliped, posterior. Scale 100 μm.

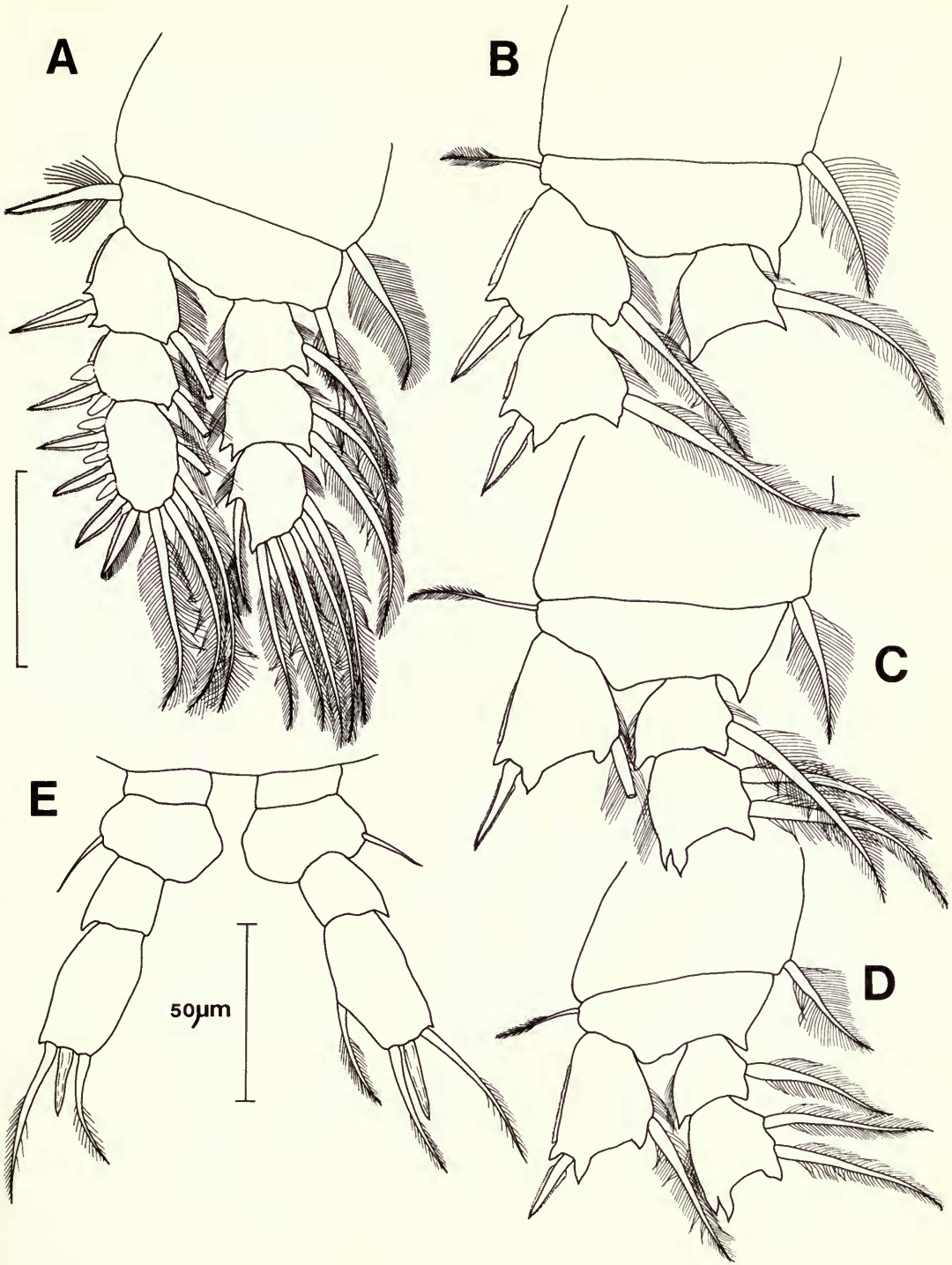

Fig. 8 *M. tetraspina.* A, leg 1, anterior; B, leg 2, anterior; C, leg 3, anterior; D, leg 4, anterior; E, leg 5, anteroventral. Scales 100 μm unless otherwise stated.

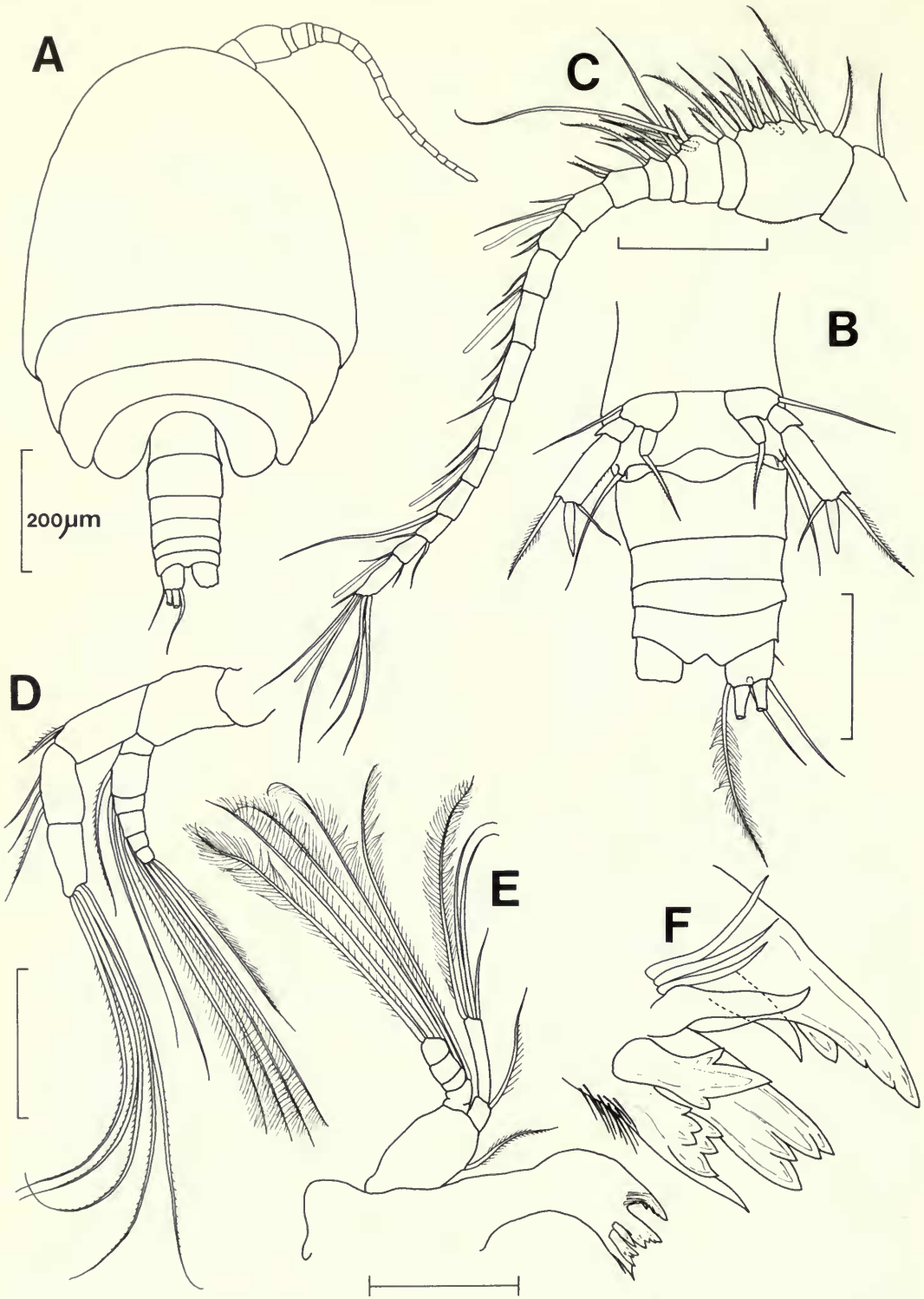

Fig. 9 *Misophriopsis dichotoma* gen. et sp. nov. Holotype ♀. A, dorsal view; B, urosome, ventral; C, antennule, dorsal; D, antenna, anterior; E, mandible, posterior; F, detail of mandibular gnathobase. Scales 100 μm unless otherwise stated.

several strong spines and a small subapical patch of pinnules. Mandibular palp comprising basis, 2-segmented endopod and an indistinctly 5-segmented exopod. Basis armed with a plumose seta midway along inner margin. Endopod segment 1 with plumose seta at inner distal angle; segment 2 elongate with 4 unequal setae on distal margin. Exopod segments 1 and 2 incompletely separated; segment 1 unarmed; segments 2 and 3 each with a plumose seta at inner distal angle; segment 4 probably with inner seta, missing from dissected appendage but its presence indicated by a scar on the surface of the segment; segment 5 with 1 inner and 2 distal margin setae.

Maxillule (Fig. 10A), gnathobase with 7 distal margin spines, 2 hirsute setae and 3 naked setae subapically on the posterior surface, and 2 plumose setae on a spinulate swelling on the anterior surface. Endite 1 short and slightly furrowed on its posterior surface, armed with 6 apical plumose setae. Endite 2 long, with 3 apical plumose setae. Outer lobe rudimentary, represented by 8 plumose setae on outer surface of segment. Maxillulary palp biramous with 2-segmented endopod and 1-segmented exopod; segment 1 of endopod fused to basis, with junction marked by 2 subapical setae. Endopod segment 1 with 4 plumose setae at inner distal angle; segment 2 with 3 naked setae arising proximal to the midpoint of the inner margin, 3 similar setae arising subapically on same margin, and 5 setae on distal margin. Exopod with 9 plumose inner and distal margin setae of varying lengths and with fringes of long pinnules proximally.

Maxilla (Fig. 10B) 6-segmented; segment 1 with 5 plumose setae on proximal endite and 3 on distal endite; segment 2 with 3 plumose setae on both proximal and distal endites; segment 3 produced medially into a curved claw armed with 2 naked setae near its base; segments 4 to 6 with a total of 7 naked setae.

Maxilliped (Fig. 10C) 7-segmented, although proximal segment showing some signs of subdivision at midlength. Segment 1 bearing 4 plumose setae and a short naked seta along inner margin, and some long pinnules proximally on outer margin; segment 2 with 3 inner margin plumose setae; segments 3 to 6 each with 2 long, unilaterally plumose setae at inner distal angle; segment 7 with 3 distal setae.

Legs 1–4 (Figs 11 A–D) biramous, with 3-segmented rami. Armature formula as follows:

	coxa	basis	endopod	exopod
leg 1	0–1	I–I	0–1;0–2;1,2,3	I–1;I–1;III,I,4
leg 2	0–1	1–0	0–1;0–2;1,2,3	I–1;I–1;III,I,5
leg 3	0–1	1–0	0–1;0–2;missing	I–1;I–1;III,I,5
leg 4	0–1	1–0	0–1;0–2;missing	I–1;I–1;III,I,5

Outer margins of all exopod segments with strips of serrated membrane. Rows of pinnules present on inner margins of all exopod segments and inner and outer margins of endopod segments. Outer margin spines of leg 1 armed bilaterally with fine strips of smooth membrane. Apical spines with short pinnules along inner margins, and strip of smooth membrane on outer margin in leg 1. Outer margin element on basis spinous on leg 1, setiform on legs 2 to 4.

Leg 5 (Fig. 11E) *biramous,* comprising unsegmented protopod, 2-segmented exopod and 1-segmented endopod. Basal seta present at outer distal angle of protopod. Exopod segment 1 unarmed, segment 2 with 3 distal margin elements, a long plumose outer seta, a median spine and an inner naked seta. Endopod with single plumose seta apically.

Leg 6 (Fig. 11F) with transverse intercoxal sclerite joining members of leg pair reduced to a slender bar. Leg comprising an outer process with a long apical seta, a median spine and an inner spinous process.

MATERIAL EXAMINED. Holotype ♀ collected at *Discovery* Stn 10379 # 37 (34°57′ N 32°55′ W) in the North Atlantic to the southwest of the Azores. Caught in RMT1+8M net system fished 23 to 56 m off the bottom in a water depth of about 3000 m. BM(NH) Registration No. 1982·139.

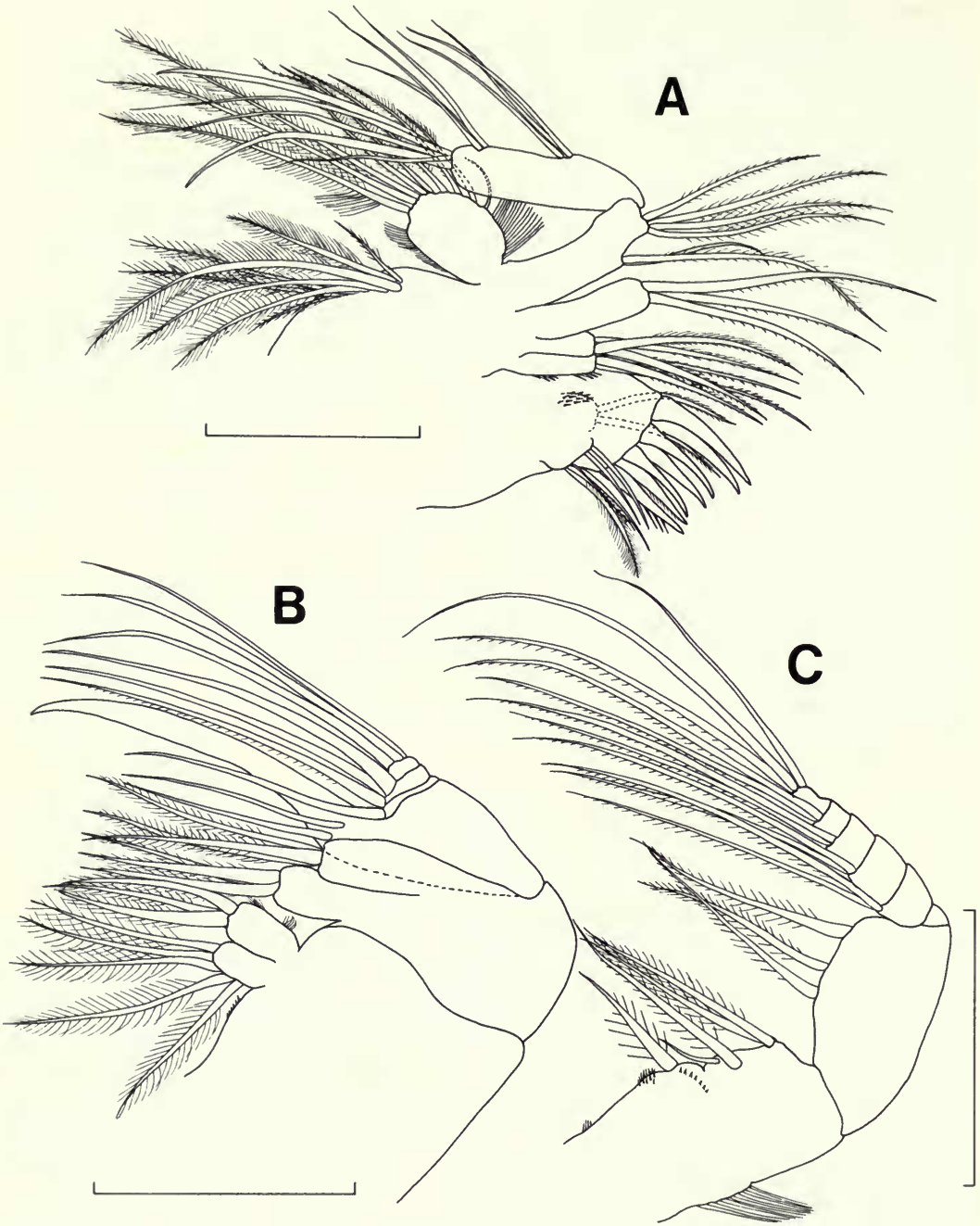

Fig. 10 *M. dichotoma.* A, maxillule, posterior; B, maxilla, anterior; C, maxilliped, anterior. Scales 100 μm.

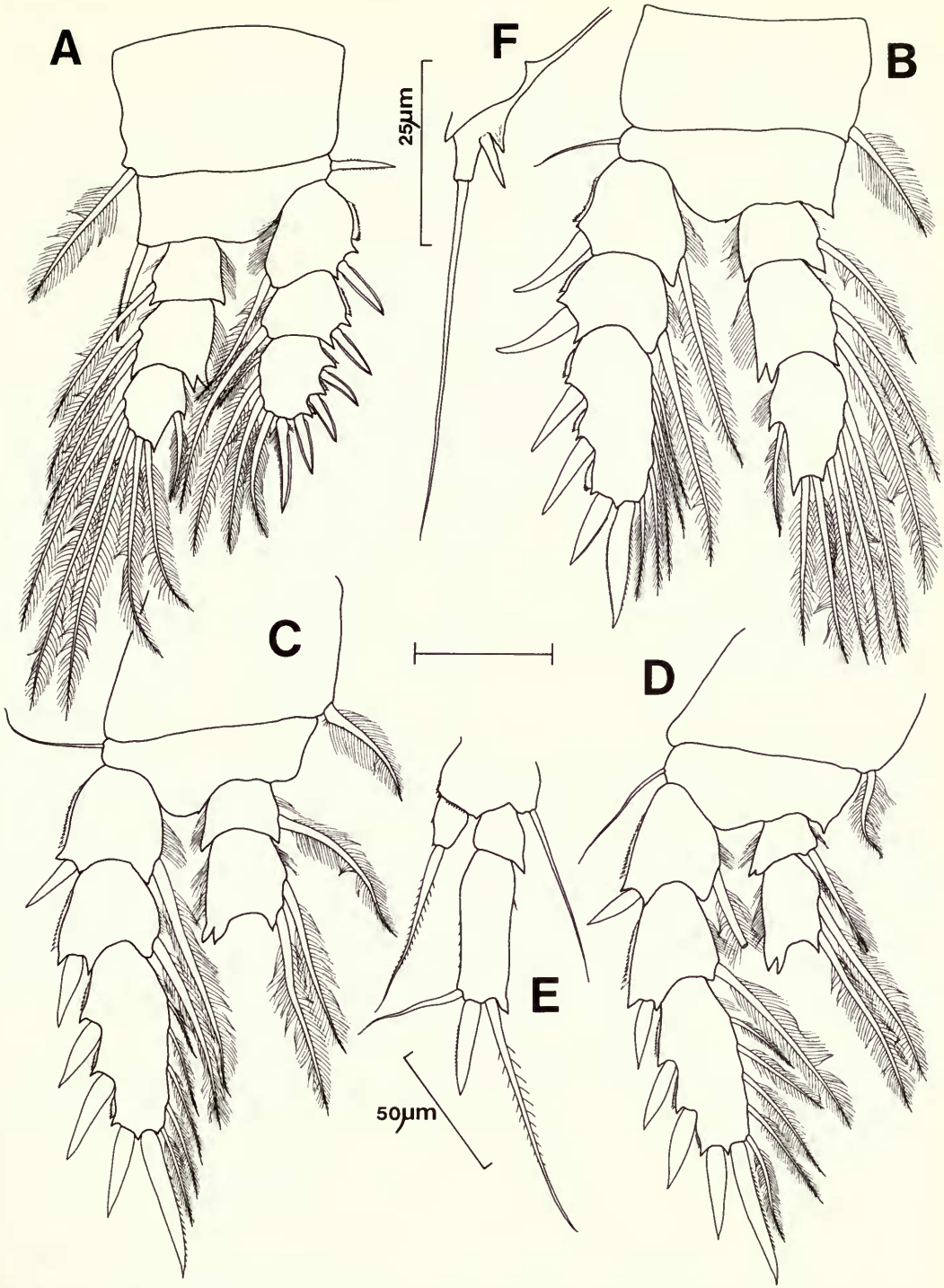

Fig. 11 *M. dichotoma.* A, leg 1, anterior; B, leg 2, anterior; C, leg 3, anterior; D, leg 4, anterior; E, leg 5, anteroventral; F, leg 6, ventral. Scales 100 µm unless otherwise stated.

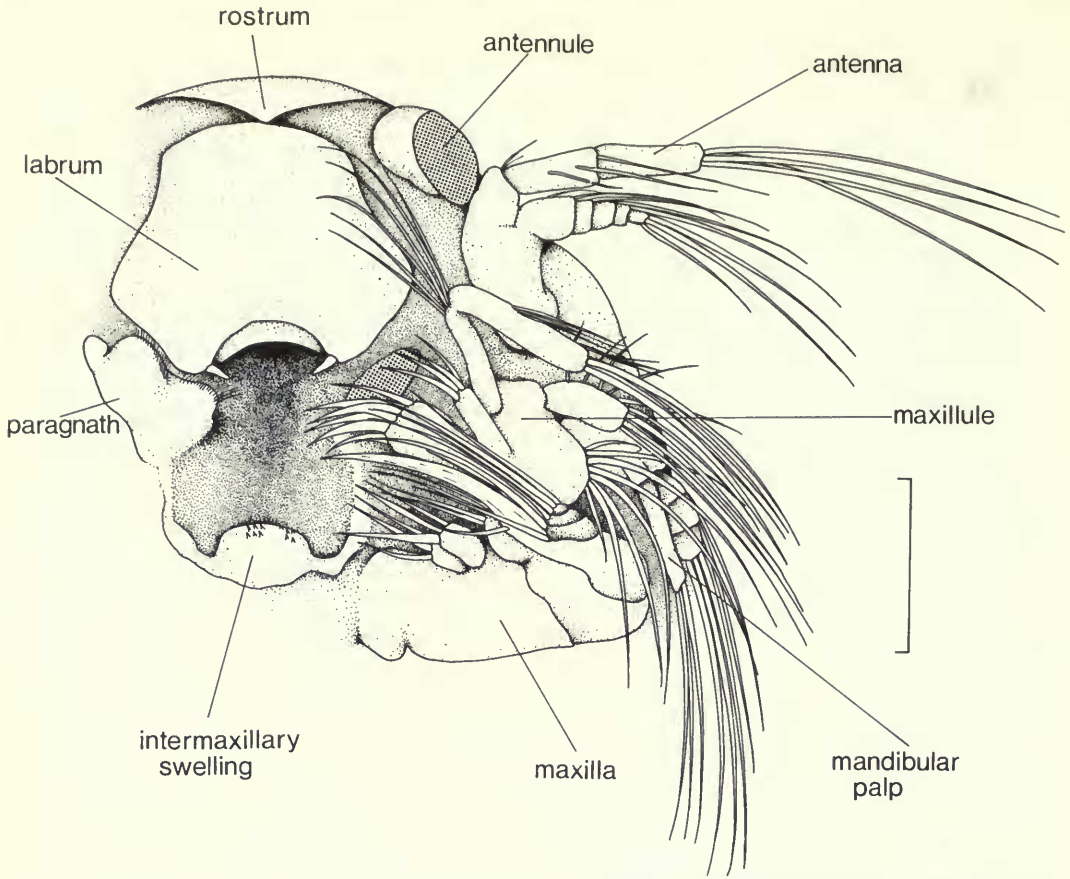

Fig. 12 *M. dichotoma.* Ventral view of mouthparts of left side, with antennule, left paragnath and mandibular gnathobase removed. Scale 100 μm.

REMARKS. The new genus differs from all known misophrioids, and from all known podopleans, in the possession of a biramous fifth leg. It also differs from other misophrioid genera in the presence of a pair of large spinous processes on the posterior margin of the labrum. The arrangement of the mouthparts (Fig. 12) is very similar to that of *Benthomisophria palliata.* The antennae and mandibular palps are both reflexed so that their setae will sweep over the areas of cone organs located laterally on the cephalosome as in *Benthomisophria.*

Key to genera and species of the Misophrioida

1. Large anteriorly directed rostrum visible in dorsal view; antennule with 25 (♂) or 27 (♀) segments. . . . . ***Archimisophria discoveryi***
   Rostrum ventrally or posteroventrally directed, not visible in dorsal view; antennule with less than 25 segments 2
2. Leg 5 biramous, with 1-segmented endopod and 2-segmented exopod . . . . . ***Misophriopsis dichotoma***
   Leg 5 uniramous, with 1 to 4 segments 3
3. Leg 5 4-segmented, antennule with 19 segments (♀) . . . . ***Misophriella tetraspina***
   Leg 5 with less than 4 segments, antennule with less than 19 segments (♀) 4
4. Leg 5 3-segmented; antennule with 13 segments (♂) or 16 segments (♀) ***Misophria pallida***
   Leg 5 2-segmented, comprising a triangular proximal segment and short distal segment; antennule with 18 (♀) or 16 (♂) segments . . . . . ***Benthomisophria palliata***
   Leg 5 1-segmented; antennule with 16 segments (♀ & ♂) . . . . . ***B. cornuta***

Discussion

These three new genera exhibit between them an unusual array of plesiomorphic characters, many of which are present in a state approaching that attributed to the hypothetical ancestor of the Copepoda as a whole (see discussion in Boxshall *et al.,* in press). The antennae, for example, are biramous with an 8-segmented exopod and a 3-segmented endopod in *Archimisophria*, and the mandibles have a well developed gnathobase plus a biramous palp with a 5-segmented exopod and 2-segmented endopod in *Misophriopsis.* The basic structure of both these limbs is the same as that proposed for the ancestral copepod. The detailed structure of the maxillule was not considered in the discussion reported by Boxshall *et al.* (in press) but in my opinion the misophrioid pattern of large gnathobase, 2 other endites, 1 setose outer lobe, a 1-segmented exopod and a 3-segmented endopod, with the first segment fused to the basis, may well be similar to that possessed by the ancestral copepod. The misophrioid maxilla comprises 6 segments, the first 2 each bear a pair of setose endites, the third a claw-like endite, and the fourth to sixth variable number of inner and distal setae. This is close to what may be considered to be the ancestral copepod pattern. The 8-segmented maxilliped of *Archimisophria* consisting of a 3-segmented protopod and 5-segmented endopod is also very similar to the 9-segmented basic copepod maxilliped favoured by Gurney (1931) in his analysis of copepod appendages.

All these misophrioid features closely approximate to those exhibited by the plesiomorphic calanoids. It is the common possession of these calanoid-like gnathostomatous mouthparts and the possession of a heart that indicates that the Misophrioida diverged from the podoplean lineage soon after its separation from the gymnoplean lineage. The discovery of a 27-segmented antennule in *Archimisophria* and of a biramous fifth leg in *Misophriopsis* clearly demonstrates that the Misophrioida has diverged less from the common ancestral stock of the Copepoda than any other podoplean group.

The possession of a biramous fifth leg is of great phylogenetic significance. The difference between the normal biramous fifth swimming leg of gymnopleans and the reduced uniramous fifth leg of podopleans led Giesbrecht (1899) to suggest the possibility that they are not homologous. Gurney (1931) rejected this and suggested that the typical uniramous leg of podopleans represents the exopod of an originally biramous limb. This interpretation has been widely adopted and the presence, in *Misophriopsis,* of a biramous fifth leg in which the endopod is reduced to a single segment bearing a single seta provides further confirmation. The fifth leg undergoes considerable reduction within the Misophrioida. In *Misophria* the endopod is represented by a single median seta on the distal margin of the unsegmented protopod, although the exopod is similar to that found in *Archimisophria.* In *Benthomisophria cornuta* the fifth leg is reduced to a single segment.

The 27-segmented antennule of female *Archimisophria* is of interest because of the considerable controversy that exists (see Boxshall *et al.,* in press) concerning the nature of this limb in the ancestral copepod. Giesbrecht (1892 & 1899) analysed the segmentation and armature of the antennules of many calanoid and other copepods in an attempt to reduce the antennule of all copepods to a common type. Giesbrecht's basic copepod antennule was 25-segmented and by studying the arrangement of the armature elements he was able to determine which segments had fused in those forms with fewer segments. This basic limb closely resembles that of *Calanus finmarchicus* Gunnerus, 1770 both in number of segments and in setation. The typical armature present on each antennulary segment is 2 setae and 1 aesthetasc, at least in the female, although one or more of these elements is often lost, most commonly the aesthetasc. Even the arrangement of these 3 elements, which Giesbrecht called a 'trithek', follows a constant pattern. One seta, the proximal seta, is positioned about midway along the anterior margin of the segment whereas the other seta, the distal seta, and the aesthetasc are positioned close together at the distal angle of the anterior margin. The typical trithek may have been different for the male, because a proximal and a distal seta plus 2 distal aesthetascs are commonly found, as for example, in *Eucalanus attenuatus* Dana, 1849. Some of the more distal segments have modified tritheks. In female *Calanus*

Table 1. The structure and armature of copepod antennules. A comparison between a gymnoplean *(Calanus finmarchicus)*, a podoplean *(Archimisophria discoveryi)* and their hypothetical common ancestral form

Calanus finmarchicus ♀																											
armature	S	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	D	D	P	P	p	A
segmentation	1		2		3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Archimisophria discoveryi ♀																											
armature	S	t	t	t	T	t	t	T	t	t	t	T	t	t	t	t	T	t	t	t	t	t	d	d	p	p	P	A
segmentation	1		2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Common ancestral pattern ♀																											
armature	S	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	D	D	P	P	P	A
segmentation	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28

Where S=single seta, T=typical trithek, t=trithek without the distal aesthetasc, D=trithek without the proximal seta, d=trithek without the proximal seta and the aesthetasc, P=trithek with a posterior margin seta instead of the proximal seta, p=trithek with a posterior seta instead of the proximal seta but without the aesthetasc, A=apical elements.

finmarchicus segments 20 and 21 have no proximal seta, segments 22, 23 and 24 have no proximal seta but have instead a distal seta on the posterior margin, and the terminal segment 25 has an increased armature of up to 6 setae and an aesthetasc (see Table 1). As Gurney (1931) noted, many calanoids possess 3 complete tritheks on the second segment and a single proximal seta plus a distal trithek on the first segment. He interpreted this as evidence that the second segment of calanoid antennules is derived from 3 fused segments and that the first segment may be derived from 2 fused segments. On the basis of this interpretation he postulated that the ancestral copepod antennule comprised 27 or possibly 28 segments. The discovery of *Archimisophria* with its 27-segmented antennules provides a remarkable corroboration of Gurney's hypothesis.

Comparison between the antennules of female *Calanus finmarchicus* and *Archimisophria discoveryi* is made in Table 1. The precise correspondence in the position of typical tritheks, denoted by T or t, and of modified tritheks, denoted by D or d and P or p, in these two taxa is remarkable as they are drawn from the 2 main copepod lineages, Gymnoplea and Podoplea. It is possible from the comparison in Table 1 to identify a common pattern from which both may be derived by reduction. I suggest that this pattern may well represent that found in the common ancestor of the Copepoda.

Functional interpretation of the unique characters exhibited by misophrioids (Boxshall, 1982 & in press) suggests that the ancestral misophrioid stock became adapted to a bathypelagic existence and to gorging as a feeding strategy. The group appears to have radiated in the deep-sea near-bottom environment and it is probable that many new misophrioid taxa will be discovered as the near-bottom community is subject to more intense study. Despite their obvious specializations the misophrioids also retain many characters of the presumed ancestral copepod stock and it is clear that they diverged from the ancestral podoplean stock soon after it had attained its characteristic division into prosome and urosome.

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